REVIEW ARTICLE

A review of the roles of forest canopy gaps

Adele Muscolo • Silvio Bagnato • Maria Sidari • Roberto Mercurio.

Abstract: Treefall gap, canopy opening caused by the death of one or more trees, is the dominant form of disturbance in many forest systems worldwide. Gaps play an important role in forest ecology helping to preserve bio- and pedo-diversity, influencing nutrient cycles, and maintaining the complex structure of the late-successional forests. Over the last 30 years, numerous reviews have been written describing gap dynamics. Here we synthesize current understanding on gap dynamics relating to tree regeneration with particular emphasis on gap characteristics considered critical to develop ecologically sustainable forest management systems and to conserve native biodiversity. Specifically, we addressed the question: how do gaps influence forest structure? From the literature reviewed, the size of gaps induces important changes in factors such as light intensity, soil humidity and soil biological properties that influence tree species regeneration and differ in gaps of different sizes. Shade-tolerant species can colonize small gaps; shade-intolerant species need large gaps for successful regeneration. Additionally, gap dynamics differ between temperate, boreal, and tropical forests, showing the importance of climate differences in driving forest regeneration. This review summarizes information of use to forest managers who design cutting regimes that mimic natural disturbances and who must consider forest structure, forest climate, and the role of natural disturbance in their designs.

Keywords: biodiversity**;** gap cutting; gap dynamic; forest management; forest restoration

Introduction

The importance of natural disturbances in shaping landscapes

Adele Muscolo (✉), Silvio Bagnato, Maria Sidari, Roberto Mercurio
Department of Agraria, "Mediterranea" University of Reggio Calabria, Feo di Vito, 89122 Reggio Calabria (Italy). Tel: 0965/897799; Fax: 0965/312827; e-mail: amuscolo@unirc.it

and influencing ecosystems is now well recognized in ecology. Disturbance, defined as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985), plays an important role in all natural ecosystems. Both small-scale (death of one or few trees) and large-scale disturbances (fires, wind storms, insect outbreaks and others) can create gaps in forest canopies that are often ideal locations and conditions for rapid plant reproduction and growth. Perhaps the most thoroughly studied impact of gap formation is how increased light helps to maintain floristic richness. Denslow (1987) theorized that the rich species diversity in tropical systems exists because each species is competitively superior for a portion of its life. Since most trees have long life spans, they exist in a variety of microenvironments as they grow. The death of a nearby tree dramatically changes light, temperature, soil moisture, and available nutrients. These conditions will favor some species, but not all. As the gap is filled, the microclimate and nutrient status slowly return to pre-disturbance levels and the resulting conditions will tend to favor a different suite of species. If a growing tree is competitively superior for a portion of its life, it will persist (Denslow 1987; Wright 2002).

On recent decades, increasing emphasis has been placed on designing silvicultural treatments that mimic natural disturbance to restore forests in a natural way, preserving biodiversity and ecosystem function while optimizing harvest and yield (Lindenmayer and Franklin 2002; Abrari Vajari et al. 2012). Gap based silviculture has recently been included in proposals for managing forests across the world and gap dynamics has been described in many temperate evergreen broadleaf (Yamamoto, 1992, 1994; Rebertus and Veblen 1993), temperate deciduous broadleaf (Runkle 2000; Yamamoto 1996), temperate coniferous (Spies et al. 1990), subalpine (e.g., Kanzaki 1984; Foster and Reiners 1986; Lertzman and Krebs 1991; Lertzman 1992; Yamamoto 1995) and boreal (Kneeshaw and Bergeron 1998) forests. In tropical forests, most gap research was based on short-term dynamics (i.e., years to decades) using large-scale permanent plot studies (e.g., Condit 1995) or on long-term dynamics (i.e., centuries to millennia) through paleoecological studies (e.g., Bush and Colinvaux 1994). In tropical forests, where the number of species is high and the range of life-history traits is broad, small-

scale heterogeneity in post-disturbance microsite conditions greatly limits the ability to anticipate future stand composition and structure (Baker et al. 2005).

The impact of gap regimes on plant population dynamics is of interest to ecologists (Naaf and Wulf 2007). Despite numerous studies carried out to identify which statistical distribution best describes gap sizes (Foster and Reiners 1986; Lertzman and Krebs 1991; Yamamoto et al. 2011), whether a gap opening is a random or clumped process in space and time (Brokaw 1985; van der Meer and Bongers 1996a; Nuske et al. 2009), if the use of a large number of gaps positively affects the forest regeneration (Cuevas 2003; Kathke and Bruelheide 2010), and how gap shapes influence microclimates and species colonization Brown 1993; van Dam 2001), numerous questions related to gap frequency, size and shape remain unanswered. In addition, more precise gap descriptions will be useful to test predictions of forest models (Chave 1999; Dubé et al. 2001; Robert 2003) and to design silvicultural systems that aim to mimic natural gap disturbance regimes (Lundquist and Beatty 2002; Schliemann and Bockheim 2011). In this review, we synthesize current understanding of gap dynamics related to tree regeneration with emphasis on gap characteristics that are considered critical to develop an ecologically sustainable forest management system. Specifically, we investigated the following questions: (1) does gap size influence forest restoration? (2) does gap size differ according to the dynamics of different forest types? Do gap shape, age and distribution affect forest regeneration dynamic? The aim is to provide insight into the capacity of gap-based silvicultural regimes to guide forest biodiversity conservation, which might be useful in legal and policy environments and to forestry managers.

Gap dynamics

In temperate forests, gap opening is the major process determining regeneration development (Runkle 1982; Sapkota et al. 2009) and a vast body of literature exists on the effects of canopy gaps on tree recruitment patterns (Yamamoto 2000; Harcombe et al. 2002; Kwit and Platt 2003; Bottero et al. 2011).

When one or few canopy trees die in a forest, mainly due to natural disturbance, this creates a hole in the canopy called a 'gap'. The term gap or canopy gap is generally used to refer to such empty areas within forest canopies. Spatial heterogeneity of canopy structure means that gaps of different size and shape exist throughout a forest stand. Over time, these spaces are filled with other trees (Watt 1947; Whitmore 1989). Gaps, once formed, do not remain static but become localized sites of regeneration and subsequent growth where tree regeneration is usually a result of released advance regeneration or recruitment from buried or dispersed seed. This phenomenon, termed 'gap dynamics' (Van der Maarel 1988; Brokaw and Busing 2000; Kimmins 2004), attracted many forest scientists and ecologists, because gap dynamics is closely related with practical forest applications such as forest conservation and natural regeneration as well as with niche partitioning and species adaptation (Yamamoto 2000). The

death of a single canopy tree or several neighboring trees introduces environmental heterogeneity to the forest ecosystem, such as changes in light levels, nutrient availability, litter depth, and regeneration microsites associated with snapped or uprooted trees. This heterogeneity plays an important role in maintaining the structure and composition in gap dynamic forests (Grubb 1977; Denslow 1980; Whitmore 1989). The components of gap dynamics, consisting of spatial and temporal factors and of magnitude, are also applicable to disturbance dynamics. Comparing the results of research on gaps and on dynamic disturbances in different geographical locations is a useful tool to predict the impact of different types of disturbance in different forest ecosystems.

Bottero et al. (2011) investigated gap dynamics in mixed beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Miller), and Norway spruce (*Picea abies* L., Karst.) old-growth forests of Lom in the Dinaric Mountains of Bosnia and Herzegovina. Their results suggested that gaps were mainly formed by endogenous senescence of single canopy trees. Exogenous disturbance agents, most likely related to wind and snow, acted mainly as secondary agents in breaking weakened trees and in expanding previously established gaps. Although the findings were partially consistent with other studies of gap disturbance processes in similar old-growth forests in central Europe, the observed gap dynamic placed the Lom core area at the end of a gradient that ranged from forests controlled by very small-scale processes to those where large, stand-replacing disturbances predominated.

Rugani et al. (2013) studied two beech forest reserves in southern Slovenia. They examined the structural characteristics of the two forest reserves based on data from sample plots and complete inventory obtained from four previous forest management plans. To gain a better understanding of disturbance dynamics, they used aerial imagery to study the characteristics of canopy gaps over an 11-year period in the Kopa forest reserve and a 20-year period in the Gorjanci forest reserve. Their results suggested that these forests were structurally heterogeneous over small spatial scales and exhibited relatively high annual rates of coverage by newly established (0.15 and 0.25%) and closed (0.08 and 0.16%) canopy gaps. New gap formation was dependant on senescent trees located throughout the reserve, leading to the conclusion that these stands were not even-sized, but rather unevenly structured. This was due to the fact that the disturbance regime was characterized by low intensity, small-scale disturbances. Fox et al. (2000) and Herwitz et al. (2000) showed changes in gap dynamics over time, concluding that the total gap area had a clear decreasing trend: smaller gaps vanished in the course of time and the larger ones tended to shrink. Meyer et al. (2000) showed that mature beech stands close gaps via vertical growth of gap-neighboring and understorey trees. The decline of the number of canopy gaps is well reflected in gap density rather than in spatial distribution (Spellmann, H. 1991).

Gap ecology

The ecological characteristics of a gap differ from those of the

surrounding forest. Gaps are brighter and warmer due to increased irradiance, and their surface soils contain more water due to the reduction in plant transpiration (Denslow 1987). Treefall gaps exhibit substantial changes in soil composition, due to differences in microclimate that affects soil microbial biomass amount and activities which in turn change soil chemical and physical properties (Denslow 1987). The degree of gap opening is correlated with many abiotic (e.g., light availability, soil and air temperature, air vapor pressure deficit, soil nutrient and water content) (van Dam 2001) and biotic factors (e.g., humus quality, micro-flora and micro-fauna, herbivore); all variables may in turn influence tree seedling establishment and development, gap floristic composition and structure (Zhang et al. 2013). Gaps also play an important role in forest ecology helping to maintain bio- and pedo-diversity and influencing nutrient cycling. Gap ecology retrospective studies have been carried out mainly by Platt and Strong (1989), Denslow and Spies (1990), Coates and Burton (1997) and McCarthy (2001). With respect to models for simulating processes in treefall gaps, recent research has been reported by Schliemann and Bockheim (2011) showing that large openings tend to have microclimates and return intervals significantly different than those of smaller treefall gaps and surrounding intact forest area, and these affect forest ecology and soil ecosystems.

Soil and air temperature

The increase in direct radiation from canopy opening increases air temperature close to the ground which in turn can increase soil temperature (Malcolm et al. 2001), causing the mortality of young tree seedlings when the topsoil temperature is >50 °C (Waring and Schlesinger 1985; Helgerson 1990). The relationship between gap size and soil temperature needs further study. Several studies in conifer stands showed no significant differences in mean air temperature during growing season between gaps of different sizes (Gray et al. 2002; Muscolo et al. 2007 a, b). In contrast, many other authors demonstrated that soil temperature increases with increasing gap size, both in coniferous stands in the Pacific Northwest, USA (44–45° N) (Gray et al. 2002), and in Southern Apennines, Italy (38° N) (Gugliotta et al. 2006; Muscolo et al. 2007 a, b). Sariyildiz (2008) found in oak, beech and chestnut stands in northeast Turkey (41° N) an inverse correlation between gap size and temperature increase. Ritter et al. (2005) and Gugliotta et al. (2006) showed that soil temperature was higher during growing season in the centre compared to the edges of gaps. But an increase in soil temperature during summer was also observed in the northern part of gaps (Bauhus 1996; Wright et al. 1998; Gray et al. 2002) in mature, deciduous and coniferous forests. These results, even if in some case controversial, show a relationship between gap size, air temperature and soil temperature.

Soil moisture

Soil moisture is a crucial factor for tree regeneration in many areas (e.g. in Mediterranean forests, Giacobbe 1958), and it is strictly related to alterations of rainfall patterns caused by climate change (IPCC 2007). The impact of gap opening is particularly significant on soil moisture content, which is higher inside gaps than under the surrounding closed canopy as observed in a wide variety of forest types: tropical forests (Vitousek and Denslow 1986; Veenendal et al. 1996; Ostertag 1998; Denslow et al. 1998); pine forests (Brockway and Outcalt 1998; Zhu et al. 2003); temperate conifer forests (Malcom et al. 2001; Gray et al. 2002; Cutini et al. 2004; Albanesi et al. 2005); and temperate hardwoods (Bauhus and Bartsch 1995; Ritter et al. 2005; Ritter and Vesterdal 2006; Gálhidy et al. 2006; Scharenbroch and Bockheim 2007a; Sariyildiz 2008**).**

The higher soil moisture content in gaps than in surrounding forest was probably due to an increase in rainfall and to a decrease in transpiration (Zirlewangen and von Wilpert 2001; Zhu et al. 2003).

Soil water conditions vary greatly according to gap sizes (Ochiai et al. 1994). In conifer forests in the Southern Apennines, soil moisture during the growing season differed between gaps of different sizes, showing the highest value in the small gaps (185-380 m^2) (Muscolo et al. 2007 a, b). In temperate hardwoods, differences in soil moisture between gaps of different size were not statistically significant (Sariyildiz 2008), suggesting that location is important in determining soil moisture and temperature differences between gaps and surrounding canopy, and contributing to the differences observed in air temperature and rainfall between temperate and tropical forests.

No differences were reported between soil moisture in gap centres and gap edges in pine stands (Palik et al. 1997; McGuire et al. 2001; Gagnon et al. 2003; Gugliotta et al. 2006). In contrast, soil moisture was greater in gap centres and decreased towards gap edges in Douglas-fir forest (44–45° N) (Gray et al. 2002), in silver fir stands (38° N) (Albanesi et al. 2005)**,** in beech-dominated forest (55° N) (47.9° N) (Ritter et al. 2005; Mihók et al. 2004) and in mixed hardwood–white pine stands (47° N) (Raymond et al. 2006), presumably due to differences in rooting density (Silver and Vogt 1993; Denslow et al. 1998).

Solar radiation

Many studies of tree regeneration have focused on the relationships between gap size, light levels and regeneration success. Poulson and Platt (1989) and Messier (1996) reported that at any geographic location, the amount of light entering the gap depends on the size and topographic position of the gaps, on the location within a gap, on the height of the surrounding canopy, and also on the sun angle and sky conditions. Numerous studies (McGuire et al. 2001; Diaci 2002; Gray et al. 2002; Zhu et al. 2003; Mihók et al. 2005; Albanesi et al. 2005; Gugliotta et al. 2006; Gálhidy et al. 2006; Muscolo et al. 2007 a , b; Raddi et al. 2009; Diaci et al. 2012) supported these findings, showing that the amount of solar radiation reaching the ground in a gap is directly related to the size of the canopy opening and also to the gap position. Higher PAR (photosynthetically active radiation) transmittance values were detected in gap centres rather than at gap edges (Canham et al. 1990; Brown 1996; Gray and Spies

1996; Palik et al. 1997; McGuire et al. 2001; Diaci 2002; Gagnon et al. 2003; Ritter et al. 2005; Gálhidy et al. 2006). A gradient of increased light from the southern to the northern edge of gaps was also reported by many researchers in the northern hemisphere during the growing season (Coates 1998, 2000; Wright et al. 1998; McGuire et al. 2001; Gray et al. 2002; Gagnon et al. 2003; Mihók et al. 2005; Raymond et al. 2006; Diaci et al. 2008). Diaci et al. (2008) and Caquet et al. (2010) found an interesting positive relationship between seedling height and light availability: with increasing light intensity and duration of light exposure, seedling height increased.

Nutrient cycling and soil organic matter turnover

In forest gaps there is a high rate of soil organic matter decomposition and mineralization, leading to increased levels of nutrients (Collins and Pickett 1987; Parsons et al. 1994; Zhang and Liang 1995; Poulson and Platt 1996; Palik et al. 1997; Denslow et al. 1998; Zhu et al. 2003; Prescott et al. 2003; Ritter 2005; Ritter and Vesterdal 2006; Muscolo et al., 2007b; Scharenbroch and Bockheim 2007a, 2008). According to Scharenbroch and Bockheim (2008) in situ surface C efflux was significantly greater in gaps, likely in response to increased solar radiation and soil temperature which, in turn, increased the mineralization of organic matter. An increase in soil temperature is generally positively related to an increase in soil microbial activities that regulate nutrient cycles in soil. Increments in ground nitrogen levels were also observed in artificially created gaps, and this may be strictly related to the enhanced growth rates of pioneer tree species (Denslow et al. 1998).

Studies of the effects of gap sizes on litter decomposition rates showed conflicting results. Lower decomposition rates in large gaps compared to small gaps or to soil under a closed canopy were observed by Zhang and Zak (1995), Prescott et al. (2003), Ritter (2005) and Sariyildiz (2008). Conversely, Denslow et al. (1998) found no significant relationships between gap size and litter decomposition rate. Other studies carried out over 4 years after gap formation in gaps of different sizes in conifer stands in the Apennines indicated that C/N ratio, an index used to monitor the decomposition of litter (Taylor et al. 1989), was greatest in small gaps (where humification processes prevailed) and lowest in large gaps (where mineralization processes prevailed) (Muscolo et al. 2007a, b; 2011). This finding suggested that small gaps were more favorable for late-successional species whereas large gaps encouraged early-successional species as *Pinus*. Considering that soil microbial biomass is either a source or sink of available nutrients and plays a critical role in nutrient transformation in terrestrial ecosystems (Singh et al. 1989), any change in microbial biomass has a direct influence on ecosystem stability and fertility (Smith et al. 1993). For these reasons, microbial biomass is always used for assessing soil quality under different types of vegetation (Groffman et al. 2001; Zeng et al. 2009) as well as for evaluating soil perturbation, restoration (Ross et al. 1982; Smith and Paul 1990) and changes induced in soils by forest management. Therefore, information on variations in soil microbial biomass is needed to improve our understanding of the effect of soil management on soil nutrient availability in gaps of different sizes compared to sites under canopy cover. Muscolo et al. (2007b) demonstrated that the greatest amount of microbial biomass and largest populations of bacteria and fungi in small gaps in pine forests contributed to more rapid and balanced turnover of organic matter and nutrients, indicating that creation of small gaps represents a silvicultural practice with minor environmental impact. QBS-ar index (biological soil quality, Parisi 2001) is based on the abundance of micro-arthropods in the soil and was measured to compare soil quality and fertility in gaps of different sizes. Blasi (2010) demonstrated that this index did not vary in soil inside gaps compared with soil under a beech canopy, suggesting that gaps did not influence micro-arthropod abundance in the context of forest ecology, and that creation of gaps as a silvicultural method was ecologically sustainable.

Biodiversity and vegetation dynamics

Gaps increase habitat diversity, structural complexity, fauna and flora species diversity (Runkle 1982, 1991; Denslow 1987; Levey 1988; Whitmore 1989; Attiwill 1994; Tews et al. 2004; Obiri and Lawes 2004; Pedersen and Howard 2004; Schnitzer et al. 2008; Wang and Liu 2011; Gray et al. 2012).

Higher species diversity was recorded in gaps than in closed forest (Denslow 1980; Sipe and Bazzaz 1995; Busing and White 1997; Schumann et al. 2003; Kumar and Ram 2005; Van Couwenberghe et al. 2010) and species exhibited niche differentiation along a gap-size gradient (Wang and Liu 2011). Zhu et al. (2003) reported that density of seedlings older than 1 year increased with increasing gap size or canopy openness (OP), suggesting that microclimate changes (light, soil water, and airflow exchange), are important in alleviating seedling competition in gaps created by thinning. This was also reported for studies of 540 m² gaps created in the Central Apennines, Italy (43° N). In 80-100 year-old silver fir (*Abies alba* Mill.) stands, shade-intolerant species were normally replaced by shade-tolerant species (Mercurio and Spampinato 2001), thus broadleaved species successfully regenerated in gap centres, while silver fir grew at gap edges (Mercurio 1994, 2000; Cutini et al. 2004).

In natural forests biodiversity probably increased shortly after gap creation and decreased with canopy closing, because gaps resemble the natural forest (in species composition) over time owing to plant succession. Several studies showed the importance of gaps in maintaining the diversity and regeneration of species within old-growth forests in subtropical (Barik et al. 1992) and southern tropical regions of India (Chandrashekara and Ramakrishnan 1993, 1994), China (Li et al. 2005; Zang and Wang 2002; Zang et al. 2005) and in temperate (Vetaas 1997) and subtropical forests of Nepal (Sapkota et al. 2009) and of North Carolina (Xi et al. 2008). In plantation forests composition and structure in gaps may be distinct from the rest of the forest, even after canopy closing. A characteristic of plantation forests is their consistently low species diversity (Coates and Burton 1997). Gaps in plantation forests can, however, provide habitat for native species to germinate, survive and grow. In plantation forest, when native tree species become canopy dominants in gaps, the

species diversity of both canopy and understory increase significantly in comparison to the original forest, potentially leading to an overall increase in biodiversity (Nakamura et al. 2005; Dupuy and Chazdon 2008). Dietze and Clark (2008) quantified the abundance, competitive ability, and interspecific variability of vegetative reproduction in 18 replicated experimental gaps in the southern Appalachians and Carolina Piedmont, USA to assess the potential role of sprouting in driving gap dynamics. In a four-year study they monitored annual rates of damaged adult survival, sprout initiation, growth, and mortality, and compared these to the performance of gap-regenerating saplings. Recruitment from sprouts constituted 26–87% of early gap regeneration and formed the dominant pathway of regeneration for some species. Sprouts from recently damaged trees also grew significantly faster than the saplings with which they competed. For all measured demographic rates (damaged tree survival, sprout initiation, number, growth, and survival) differences among species were large and consistent across sites, suggesting that vegetative reproduction was an important and non-neutral process in shaping community composition. Sprouting ability did not correlate strongly with other life-history trade-offs, thus sprouting potentially provided an alternate trait axis in promoting diversity. Rouvinen and Kouki (2011) examined the effects of gap size and canopy openness (experimentally manipulated) on within-gap variation and within-gap microhabitat variability (disturbed vs. undisturbed forest floor) in field settings of *Pinus sylvestris* L. dominated forest. Natural and artificial (direct seeding of silver birch *Betula pendula* Roth) tree regeneration and development was monitored both on disturbed (scarified soil patches) and undisturbed forest floor during three growing seasons. Results showed that gaps can be valuable in diversifying stand structure but to be successful and rapid, tree regeneration needs disturbed forest floor. Pine regenerated abundantly but birch had clearly lower regeneration, especially in small gaps.

Thus, considering the regeneration pattern, it is possible to predict with high accuracy which species can successfully establish and grow in a given canopy gaps (Qin et al. 2011).

Gap origins, characteristics and geometry

Gap origins

Natural gap formation is generally attributed to wind, snowfall, insects, diseases, acid deposition, drought, climate change, and fires. However, several studies identified other factors responsible for gap formation, including soil properties such as shallow depth to bedrock, high water table and poor drainage, and presence of coarse fragments (Liu and Hytteborn 1991; Bockheim 1997; Lin et al. 2004; Woods 2004; Scharenbroch and Bockheim 2007b), tree species characteristics such as dbh (diameter at breast height), flat-rooted pattern (e.g., *Tsuga, Picea,* and *Abies*), and tap-rooted pattern (e.g., *Pinus, Quercus,* and *Acer*) (Liu and Hytteborn 1991; Clinton and Baker 2000; Lin et al. 2004).

In natural gaps the tree generally remains in the gap and, as a consequence of wind throw, often with the root ball exhumed

from the soil, but attached to the tree.

Artificial gaps result from silvicultural treatments. Stumps and root systems are normally left in the ground. Therefore soil disruption and biomass removal are different in man-made and natural gaps. Felling a single tree results in a gap formation similar to the natural situation. But usually more trees are felled in a small area and thus the gaps are larger, resulting in far higher light levels.

Gap size

Gap size is often used as an indicator of environmental heterogeneity and resource sequestration in gaps. Gap size reflects the magnitude of the disturbance (i.e. the type, number and size of falls, Ogden et al. 1991; Midgley et al. 1995; van der Meer and Bongers 1996; Lima et al. 2008), which has a direct influence on gap microclimate and understory damage levels (Zhu et al. 2007).

The size of a gap can strongly influence vegetation growth, nutrient cycling (Zhang and Zak 1995; Gray et al. 2002; Muscolo et al. 2007b) and can have considerable effect on a number of biological processes. McCarthy (2001) reported that gap disturbance determines forest structure and processes to a greater extent than previously assumed, showing that boreal forests dominated by the shade-tolerant fir (*Abies*) – spruce (*Picea*) complex are particularly well-adapted to the development of long-term, old-growth continuity in the absence of large-scale disturbance. Coates (2002) showed that seedling recruitment success in multispecies northern latitude forests varied as a function of mature tree canopy cover, gap size and position in a gap. Recruitment was abundant within canopy gaps across a wide range of gap sizes (20–5000 m^2), but recruit numbers dropped off rapidly under the closed forest canopy and in the open conditions of clearcuts. Inside canopy gaps, recruitment was similar in each gap position in small gaps (<300 m^2). Conversely, in larger gaps in northern latitude forests, recruitment increased from the sunny northern to the shaded southern portions of gaps. This was true for all tree species regardless of their shade tolerance. There was no evidence of gap partitioning by any of the tree species during the regeneration phase, suggesting that adaptation to the subtleties of gap size during early recruitment were not well developed in these tree species. Favorable locations for emergence and early establishment of germinates were less favorable for growth and survival of established seedlings. Tree abundance and species diversity appeared to be controlled more by differentiation between growth and survival niches than by regeneration niches. From the perspective of forest management, abundant natural regeneration of all dominant tree species of these mixed-species forests could be obtained after partial cutting

Schliemann and Bockheim (2011) suggested that the maximum gap size should be set at 1000 m^2. Larger openings tended to have microclimates and return intervals significantly different from those of smaller tree-fall gaps. Subsequently, Kern et al. (2013) evaluated the influence of harvest-created gap sizes (6, 10, 20, 30, and 46 m diameter gaps and uncut references) over 12 growing seasons on planted tree seedling growth and survival for four tree species that tend to experience poor recruitment in both

managed and unmanaged northern hardwood forests in eastern North America. All four of their species grew taller with increasing gap size, while survival was highest in intermediate gap sizes. Although gap size had statistically significant effects on growth and survival, the magnitude of the effects were modest. This study highlights the management challenges of using gap size as a tool to influence future forest composition in forests with overly abundant deer and pervasive shrub layers, and underscores the importance of silvicultural prescriptions that include measures for reducing these impacts.

Gap size and gap age are correlated with each other and give important information for sustainable forest ecosystem management. Diaci et al. (2012) estimated that beech recruitment generally needed 100 years or more to reach 20 m in height and fill gaps. In an old Birch forest of the dinaric mountains, Diaci et al. (2012) found that gaps of 5–15 m in diameter will fill in 5–40 years while medium gaps of average size of about 200–300 m^2 require around 30–60 years for closure. Conversely, in temperate forests, a negative relationship was observed between seedling height and gap size, suggesting that larger gaps will be filled in less time, due to reduced seedling competition for light, nutrients and water than in small gaps (Bullock 2000). Gap size obviously differs with respect to tree size and crown dimensions, and the differences depend also on single- or multiple-tree falls, and on gap age. Zhu et al. (2014) showed that regeneration density exhibited a significantly positive correlation with gap size providing quantitative evidence of the large effect of gaps on increasing regeneration by woody species.

It has been well established that gap size is the major factor determining tree species composition. Among other factors, gap size often determines whether the available growing space will be occupied by early or late successional species (Denslow 1987). Shade-intolerant species or early-successional species are often recruited only in the larger gaps and are usually established after gap formation, or in young gaps where more light is available (Canham 1989; Yamamoto 1992; Coates and Burton 1997; Mc Carthy 2001; Obiri and Lawes 2004; Nagel et al. 2010). According to Whitmore (1982) 1000 m^2 represents the minimum gap size needed for successful regeneration of shade-intolerant species. In contrast, Busing (1994), studying old-growth Appalachian cove forests, determined that a gap size of 400 m^2 was the threshold below which intolerant species were unable to establish.

If we consider that seedling growth and density of shade-intolerant species increased significantly with increasing gap size in *Eucalyptus regnans* (Van de Meer et al. 1999) and in *Pinus thumbergii* (Zhu et al. 2003) the statement of Ciancio et al. (2006) that a pionier species like *Pinus laricio* could survive in gaps of 60–100 m^2 is inconsistent. Indeed, Zhu et al. (2003) reported that although *P. thunbergii* seeds germinated in small gaps even under a closed canopy, a minimum gap ratio ≥1.0 (gap diameter to stand height) was required for survival and development to seedling stage, and a gap ratio ≥1.5 was needed for further development to sapling stage. Garbarino et al. (2012) reported that early successional and shade-intolerant species such as sycamore maple (*Acer pseudoplatanus*) and rowan (*Sorbus aucuparia*), were present only in larger gaps in a Bosnian old-growth forest.

Shade-tolerant species or late-successional species grew better in small or older gaps (Canham 1989; Obiri and Lawes 2004; Nagel et al. 2010; Wang and Liu 2011). In general, shade-tolerant species, usually existing as advanced regeneration, have a great chance to respond to small gap openings. The physiological and morphological plasticity of shade-tolerant species allows rapid response to increased light environments. Smaller gaps in stands of pionier species favor late successional species that are frequently native (Van der Meer et al. 1999; Gugliotta et al. 2003, 2006; Kint et al. 2006; Muscolo et al. 2011). Large openings (>1000 m^2), created through cataclysm (fires, cyclones, downdrafts, mass earth movements), have differenct characteristics that treefall gaps. In particular, very large openings reduced shading from surrounding trees and consequently had higher solar radiation and soil temperature than small openings (Schliemann and Bockheim 2011).

The ratio between gap diameter and the height of the tallest surrounding trees (d/h ratio) should not exceed 1-1.5 (Cappelli 1988, Piussi 1994; Del Favero 2010). The seedlings of different tree species require different amounts of light to grow successfully. Shade-tolerant species such as western hemlock can survive under relatively dense forest canopies where light-demanding species such as larches cannot. Malcom et al. (2001) related gap size, in particular d/h ratio, to the regeneration of species with different sensitivity to light. Their results showed that a d/h ratio > 2 is optimal for the regeneration of shade-intolerant species (*Larix* sp. and *Pinus* sp.), a d/h ratio ranging between 1.0 and 2.0 was ideal for intermediate shade-tolerant species (Douglas fir) while a ratio <1.0 was required for shade-tolerant species (*Abies* sp.). Nyland (2002) suggested that gap openings should be 1 or 2 times wider than the height of the surrounding trees for a better tree regeneration.

In short, the above findings suggest that gap size had a strong influence on tree species regeneration, especially through its affects on light intensity and soil humidity. Tree species regeneration is different in gaps of different sizes and species-specific survival and growth strategies are related to gap size and type of vegetation. Thus, gaps of different sizes can be considered one of the most important mechanisms for the maintenance of tree species diversity in forests.

Gap shape

Gap shape distributions are important descriptors of the forest disturbance regime. Gap shape substantially influences gap microclimate and can reflect the direction and the architecture of the falling tree (Brown 1993; Salvador-Van Eysenrode et al. 1998). Gap shape is very important in determining site resource availability (Canham et al. 1990; Lertzman and Krebs 1991). In general, irregular narrow gaps will receive far less p…. a….. r….. (PAR) at ground level than circular gaps of the same size. Numerous shapes have been recognized, including dumb-bell or chablis (Oldeman 1978), ellipse (Runkle 1981), and triangle (Salvador-Van Eysenrode et al. 1998).

However, gaps often are irregularly shaped (Lertzman and Krebs 1991; Battles et al. 1996; Gagnon et al. 2004). Kotanen

(1997) suggested that species with poor dispersal ability were slower to colonize larger or rounder gaps than smaller or less circular gaps. Conversely, dispersive and seed-banking species were less sensitive than poor dispersers to gap size and shape, and less confined to gap edges. He found that species reproducing largely by clonal growth (bulbs and perennial graminoids) were initially most sensitive to gap size and (to a lesser extent) to shape, reaching their greatest abundance in small and (or) rectangular openings. Species relying on seed dispersal (annual grasses) also tended to do the best in smaller gaps, but were less concentrated near gap edges. Species relying on seed dormancy were least sensitive to gap size, shape, and distance from an edge. These results suggest that species respond to gap size and shape in ways consistent with their reproductive biology, highlighting the importance of the dimensions of gaps in driving plant community composition.

When gap shapes are more irregular, the effects of edge on the inner-gap environment become more pronounced because of the increased competition for both aboveground (light) and belowground (water, nutrients) resources (Gagnon et al. 2004). However, even if natural gaps are irregularly shaped (Spies et al. 1990; Lertzman and Krebs 1991; Battles et al. 1996; Gagnon et al., 2004; Schliemann and Bockheim 2011) most are elliptical or circular (Brokaw 1985; Clinton et al. 1993; Goldblum 1997) and fewer are dumbbell-shaped "chablis" (Oldeman 1978). Garbarino et al. (2012) confirmed that gap geometry was related to regeneration composition, showing that early successional and shade-intolerant species, such as sycamore maple and rowan, were positively associated with large (area and perimeter) and elongated gaps, while numbers of European beech saplings were not influenced by gap size but were weakly associated with gap filler basal area probably because this species is shade-tolerant only in the first stages of its life. The different pattern observed for rowan seedlings and saplings was probably due to the fact that this species is shade-tolerant only in the first stages of its life. Based on these results related to the observation of natural regeneration in natural gaps of different shapes, the main man-made gap shapes adopted in silvicultural management are:

－circular (De Philippis 1948; Perrin 1954; Cappelli 1988; Piussi 1994; Malcom et al. 2001; Del Favero 2010);

－elliptical, more appropriate to limit the effects of wind turbulences (Runkle 1981; Del Favero 2010); and

－square (Cappelli 1988; Piussi 1994; Del Favero 2010).

Gap age

Over time, microsite characteristics within gaps slowly revert to those of a closed forest and consequently gap age, strictly correlated with gap size, is an important parameter to be considered in forest management. Forest dynamics are driven by continuous disturbances and are characterized by quasi-equilibrium structure. Thus, gap age is an important driver of forest change prior to a complex stage of development.

Many authors reported positive correlation between regeneration density and gap age in mature stands, and also a negative correlation in old-growth stands that reflected differences in under-story light conditions and forest structure. In mature stands where tree saplings are sparse, gaps can continue to be sites of new seedling establishment because understory resources are still available in gaps surrounded by relatively open upper and mid canopy layers. Conversely, in old-growth stands, where tall trees surround many gaps, light and below ground resources may be so low that the first seedlings established in the gaps preempt resources and retard further seedling establishment. These results were confirmed in Cameroon forest by Bongjoh and Mama (1999), who found a positive correlation between gap age and regeneration, suggesting that among 5 forest blocks of aged classes (1, 3, 6, 9, 12 years) species and seedling densities were highest in 1 year-old gaps. Thus, in relatively young forests, gaps provide the mechanisms for stands to develop complex structures, and can be used to explain patterns of shifting species composition in secondary forests (Hart and Grissino-Mayer 2009). Young gaps, considered small-scale disturbances, regulate species replacement patterns and create transitional forests. In summary, forest productivity decreases in the mature gaps due to increased competition for limiting growth resources, while productivity increases in newly formed gaps. Newly formed microsites initially offer competitor-free space, but with increasing gap age, the establishment of species is precluded by resource competition. In conclusion, small-scale disturbance is recommended in forest management because it produces forest gaps which increase understory heterogeneity improving forest health and the dynamics of mature and old growth forest (Caron et al. 2009; Kirchner et al. 2011).

Spatial and temporal distribution of gaps

In managed forests, gap density is reported as the number of gaps created per hectare, while in unmanaged forests it is the number of gaps intersected by transects (Fajardo and de Graaf 2004). Gaps can be geometric-systematic (one gap every × m along straight lines), or irregularly spaced in relation to stand age, structure and dynamics, or to the distribution of forest roads. Frequency of gap creation has important consequences for species composition and forest structure. The rate of gap openings in natural mature temperate forests ranges from 0.5 to 2.0% per year (Brokaw 1985; Runkle 1985). The interval of gap disturbances in northeastern North America is usually in the range of 50-200 years (Runkle 1982; Seymour et al. 2002). Gap turnover time (mean time between successive creations of gap area at any one point in the forest, Brokaw 1985) is dependent on the rate of gap infilling, or the recruitment and growth of seedlings in the gaps. One rule should be observed: never open a new series of gaps if the previous ones are not completely regenerated. In temperate conifer stands, average seedling density below 0.5/m^2 is considered insufficient to ensure stand regeneration and supplemental planting is indicated. Marthews et al. (2008) showed that spatial gap distributions determine direct light regimes in time and space, increasing germination and emergence of seedlings. Sapkota et al. (2009) investigated gap spatial distribution, advanced regeneration and stand structure of five *Shorea robusta*-dominated forests in 25 1-ha plots subject to disturbances of dif-

ferent intensities. The overall stand density changed quadratically across the disturbance gradient. A strong inverse relationship was found between overall stand density and diameter class in the least disturbed and moderately disturbed forests. Individual species showed different responses to disturbance ranging from 'tolerant' (*Shorea robusta*, *Lagerstroemia parviflora* and *Symplocos* spp.) to 'sensitive' (*Trewia nudiflora*, *Adina cardifolia* and *Terminalia alata*). They suggested that moderate disturbance intensity not only ensures high stand density, but also enhances the advanced regeneration of important tree species

Conclusions

Forest management that approximates nature appears to be a flexible toolbox in which creation of gaps is a useful tool to secure sustainable forest development. This tool mimics natural openings of various sizes that follow moderate disturbance events. This review provides information needed to design a management system that mimics natural disturbance regimes, focusing on the importance of gap size, shape and age, and also the influence of canopy composition and structure on gap size, shape, and frequency, and noting that gap characteristics affect seedling establishment and thus future canopy composition.

Future gap research should consider the primary cover type and the aerial extent of gaps in the system. Gap-cutting silviculture might yield higher diversity in tree species composition and better forest structure. From an ecological point of view, the range of different gap sizes can create diverse habitats from which fauna can also benefit. In addition, gap-cutting systems might provide higher landscape values by scheduling cuts over time and space. A gap-cutting system is particularly suited to the restoration of forest stands in protected areas. Further investigation of soil processes, including organic matter trends, composition and activity of microbial biomass, and soil characteristics, would greatly improve overall understanding of gap dynamics and their impacts on the forest as a whole.

References

Abrari Vajari K, Jalilvand H, Pourmajidian MR, Espahbodi K, Moshki A. 2012. Effect of canopy gap size and ecological factors on species diversity and beech seedlings in managed beech stands in Hyrcanian forests. *Journal of Forestry Research*, 23: 217–222.

Albanesi E, Gugliotta OI, Mercurio R. 2005. Effects of gap size and within-gap position on seedlings establishment in Silver fir stands. *Forest@* 2, 358–366 [online] URL: http:www.sisef.it/.

Attiwill PM. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management,* 63: 247–300.

Baker PJ, Bunyavejchewin S, Oliver CD, Ashton PS. 2005. Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecological Monographs*, 75: 317–343.

Barik SK, Pandey HN, Tripathi RS, Rao P. 1992. Microenvironmental variability and species-diversity in treefall gaps in a subtropical broadleaved forest. *Vegetatio,* 103: 31–40.

Bauhus J. 1996. C and N mineralization in an acid forest soil along a gap-stand gradient. *Soil Biology and Biochemistry*, 28: 923–932.

Bauhus J, Bartsch N. 1995. Mechanisms for carbon and nutrient release and retention in beech forest gaps. I. Microclimate, water balance and seepage water chemistry. *Plant and Soil,* 169: 579–584.

Blasi S. 2010. Assessment of human impact on the community of soil microarthropods in some forest areas of Central Italy. P 12. Dissertation, University of Tuscia Viterbo Italy.

Bockheim JG. 1997. Soils in a hemlock-hardwood ecosystem mosaic in the Southern Lake Superior Uplands. *Canadian Journal of Forest Research,* 27: 147–1153.

Bongjoh CA, Mama N. 1999. Early regeneration of commercial timber species in a logged-over forest of southern Cameroon. Seminar FORAFRI Libreville - Session 2: Knowledge Ecosystem, 1-9.

Bottero A, Garbarino M, Dukic V, Goveda, Z, Lingu, E, Nagel TA. Motta R. 2011. Gap-phase dynamics in the old-growth forest of Lom, Bosnia and Herzegovina. *Silva fennica*, 45: 875–887.

Brokaw NVL. 1985. Treefalls, regrowth and community structure in tropical forests. *In:* S.A. Pickett and D.C. White (eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Orlando: Academic Press, Inc., pp. 53–69.

Brokaw NVL, Busing RT. 2000. Niche *versus* chance and tree diversity in forest gaps. *Trends in Ecology Evolution*, 15: 183–189

Brockway DG, Outcalt KW. 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. *Forest Ecology and Management*, 106: 125–139.

Brown N. 1996. A gradient of seedling growth from the centre of a tropical rain forest canopy gap. *Forest Ecology and Management*, 82: 239–244.

Brown N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *Journal of Tropical Ecology*, 9: 153–168.

Bullock JM 2000. Gaps and seedling colonization. *In*: Michael Fenner, editor. Seeds: *The Ecology of Regeneration in Plant Communities*. Wallingford, UK: CABI Publishing, p. 375–95.

Bush M. Colinvaux PA. 1994. Tropical forest disturbance: paleoecological records from Darien, Panama. *Ecology,* 75: 1761–1768.

Busing RT. 1994. Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. *Vegetatio*, 115: 19–27.

Busing RT, White PS. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. *Oikos,* 78: 562–568.

Canham CD. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology,* 70: 548–550.

Cappelli M. 1988. *Selvicoltura Generale*. Edagricole, Bologna.

Caquet B, Montpied P, Dreyer E, Epron D, Collet C. 2010. Response to canopy opening does not act as a filter to *Fagus sylvatica* and *Acer* sp. advance regeneration in a mixed temperate forest. *Annals of Forest Science,* 67: 105-116. http://dx.doi.org/10.1051/forest/2009086.

Caron MN, Kneeshaw DD, Grandpré DE, Kahanen H, Kuuluvainen T. 2009. Canopy gap characteristics and disturbance dynamics in old-growth *Picea abies* stands in Northern Fennoscandia: Is the forest in quasi-equilibrium? *Annales Botanici Fennici,* 46: 251–262.

Chandrashekara UM, Ramakrishnan PS. 1993. Gap phase regeneration of tree species of differing successional status in a humid tropical forest of Kerala, India. *Journal of Bioscience,* 18: 279–290.

Chandrashekara UM, Ramakrishnan PS. 1994. Successional patterns and gap

phase dynamics of a humid tropical forest of the Western Ghats of Kerala, India: ground vegetation, biomass, productivity and nutrient cycling. *Forest Ecology and Management*, **70:** 23−40.

Chave J. 1999. Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecological Models*, **124:** 233−254.

Ciancio O, Iovino F, Menguzzato G, Nicolaci A, Nocentini S. 2006. Structure and growth of a small group selection forest of calabrian pine in Southern Italy: A hypothesis for continuous cover forestry based on traditional silviculture. *Forest Ecology and Management*, **224:** 229−234.

Clinton BD, Baker .R. 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. *Forest Ecology and Management*, **126:** 51−60.

Clinton BD, Boring LR, Swank WT. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology,* **74:** 1551−1558.

Coates KD- 1998. *Tree species response to gap formation in partially-cut interior cedar–hemlock forests of northwestern British Columbia*. Dissertation, University of British Columbia.

Coates KD. 2000. Conifer seedling response to northern temperate canopy gaps. *Forest Ecology and Management*, **127:** 249−269.

Coates KD. 2002. Tree recruitment in gaps of various size, clear-cut and undisturbed mixed forest of interior British Columbia, *Canada. Forest Ecology and Management,* **155:** 387−398.

Coates KD, Burton PJ. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management*, **99:** 337−354.

Collins BS, Pickett STA. 1987. Influence of canopy opening on the environment and herb layer in a Northern Hardwoods Forest. *Vegetatio,* **70:** 3-10.

Condit R. 1995. Research in large, long-term tropical forest plots. *Trends in Ecological Evolution,* **10:** 18−22.

Connell JH. 1978. Diversity in tropical rain forests and coral reef. *Science,* **199:** 1302−1310.

Cuevas JG. 2003. Gap characteristics in relation to forest structure and implications for southern beech forest dynamics. *Canadian Journal of Forest Research*, **33:** 1915−1922.

Cutini A, Gamba C, Mercurio R, Modica G., Piovanelli, C., Simoncini, S., 2004. Osservazioni ecologiche su tagli a buche nelle abetine del Parco Nazionale delle Foreste Casentinesi. *Annals of Istitute Sperior of Selviculture*, **31:** 27−38.

Dietze MC, Clark JS. 2008. Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. *Ecological Monograph,* **78:** 331−347. http://dx.doi.org/10.1890/07-0271.1.

Del Favero R. 2010. I boschi delle regioni dell'Italia centrale. Cleup, Padova.

Denslow JS. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* (supplement) **12:** 47−55.

Denslow JS. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematic*, **18:** 431−451.

Denslow JS, Ellison AM, Sanford RE. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology*, **86:** 597−609.

Denslow JS, Schultz JC, Vitousek PM, Strain BR. 1990. Growth responses of tropical shrubs to tree fall gap environments. *Ecology*, **71:** 165−179.

Diaci J. 2002. Regeneration dynamics in a Norway spruce plantation on a silver fir-beech forest site in the Slovenian Alps. *Forest Ecology and Management*, **161:** 27−38.

Diaci J, Gyoerek N, Gliha J, Nagel TA. 2008. Response of *Quercus robur* L. seedlings to north-south asymmetry of light within gaps in floodplain forests of Slovenia. *Annals of Forest Science*, **65:** 105−110. http://link.springer.com/article/10.1051%2Fforest%3A2007077.

Diaci J, Adamic T, Rozman A. 2012. Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: Influences of light regime, herb competition and browsing. *Forest Ecology and Management,* **285:** 20−28.

Dubé P, Fortin MJ, Canham CD, Marceau DJ. 2001. Quantifying gap dynamics at the patch mosaic level using a spatially-explicit model of a northern hardwood forest ecosystem. *Ecological Models,* **142:** 39−60.

Dupuy JM, Chazdon RL. 2008. Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. *Forest Ecology and Management*, **255:** 3716−3725.

Fajardo A, de Graaf R. 2004. Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile. *Plant Ecology,* **173:** 95−105.

Foster JR, Reiners WA. 1986. Size distribution and expansion of canopy gaps in a northern Appalachian spruce–fir forest. *Vegetatio*, **68:** 109−114.

Fox TJ, Knutson MG, Hines RK. 2000. Mapping forest canopy gaps using air-photo interpretation and ground surveys. *Wildlife Society Bulletin* **28**(4): 882−889.

Gagnon JL, Jokela EJ, Moser WK, Huber DA. 2003. Dynamics of artificial regeneration in gaps within a longleaf pine flatwoods ecosystem. *Forest Ecology and Management,* **172:** 133−144.

Gagnon JL, Jokela EJ, Moser WK, Huber DA. 2004. Characteristics of gaps and natural regeneration in mature longleaf pine flatwoods ecosystems. *Forest Ecology and Management,* **187:** 373−380.

Gálhidy L, Mihók B, Hagyó A, Rajkai K, Standovár T. 2006. Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. *Plant Ecolology* **183:** 133−145.

Garbarino M, Borgogno Mondino E, Lingua E, Nagel TA, Dukić V, Govedar Z, Motta R. 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. *Annals of Forest Science* **69:** 617−625.

Goldblum D. 1997. The effects of treefall gaps on under story vegetation in New York State. *Journal of Vegetation Science*, **8:** 125−132.

Gray AN, Spies TA. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. *Journal of Ecology*, **84:** 635−645.

Gray AN, Spies TA, Easter MJ. 2002. Microclimate and soil moisture responses to gap formation in coastal Douglas-fir forests. *Canadian Journal of Forest Research*, **32:** 332-343.

Gray AN, Spies TA, Pabst RJ. 2012. Canopy gaps affect long-term patterns of tree growth and mortality in mature and old-growth forests in the Pacific Northwest. *Forest Ecology and Management,* **281:** 111−120.

Groffman PM, McDowell WH, Myers JC, Merriam JL. 2001. Soil microbial biomass and activity in tropical riparian forests. *Soil Biology and Biochemistry*, **33:** 1339−48.

Gugliotta OI, Mercurio R. 2003. First observations of cuts holes in the pine forests of black pine in Abruzzo. *Monti e Boschi'* **54:** 18−21.

Gugliotta OI., Mercurio R, Albanesi E. 2006. Dynamics of natural regeneration in a hole cut in the pine forests of Corsican pine (Pinus laricio Poiret) of the southern Apennines. *Forest@,* **3:** 380-386. [online] URL: http:www.sisef.it/.

Harcombe PA, Bill CJ, Fulton M, Glitzenstein JS, Marks PL, Elsik IS. 2002. Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. *Journal of Ecology*, **90:** 947−957.

Hart JL, Grissino-Mayer HD. 2009. Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA. *Plant Ecology*, **201:** 131−146.

Helgerson OT. 1990. Heat damage in tree seedlings and its prevention. *New Forests,* **3:** 333−358.

Herwitz SR, Sandler B, Slye RE. 2000. Twenty-one years of crown area

change in the Jasper Ridge Biological Preserve based on georeferenced multitemporal aerial photographs. *International Journal of Remote Sensing,* **21**(1): 45−60.

I.P.C.C. 2007. Fourth assessment report of the intergovernmental panel on climate change. Cambridge, United Kingdom and New York: Cambridge University Press.

Kanzaki M. 1984. Regeneration in subalpine coniferous forests. I. Mosaic structure and regeneration process in a *Tsuga diversifolia* forest. *Botanical Magazine Tokyo,* **97**: 297−311.

Kathke S, Bruelheide H. 2010. Gap dynamics in a near-natural spruce forest at Mt Brocken, Germany. *Forest Ecology and Management,* **259**: 624−632.

Kern CC, Montgomery RA, Reich PB, Strong TF. 2013. Canopy gap size influences niche partitioning of the ground-layer plant community in a northern temperate forest. *Journal of Plant Ecology,* **6**: 101−112.

Kimmins JP. 2004. Forest Ecology, third ed. Prentice Hall, Upper Staddle River.

Kint V, Geudens G, Mohren GMJ, Lust N. 2006. Silvicultural interpretation of natural vegetation dynamics in ageing Scots pine stands for their conversion into mixed broadleaved stands. *Forest Ecology and Management,* **223**: 363−370.

Kirchner K, Kathke S, Bruelheide H. 2011. The interaction of gap age and microsite for herb layer species in a near-natural spruce forest. *Journal of Vegetation Science,* **22**: 85−95.

Kneeshaw DD, Bergeron Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology,* **79**: 783−794.

Kotanen PM. 1997. Effects of gap area and shape on recolonization by grassland plants with differing reproductive strategies. *Canadian Journal of Botany,* **75**: 352−361.

Kumar A, Ram J. 2005. Anthropogenic disturbances and plant biodiversity in forests of Uttaranchal, central Himalaya. *Biodiversity Conservation,* **14**: 309−331.

Kwit C, Platt WJ. 2003. Disturbance history influences regeneration of non-pioneer understory trees. *Ecology,* **84**: 2575−2581.

Lertzman KP, Krebs CJ. 1991. Gap-phase structure of a subalpine old-growth forest. *Canadian Journal of Forest Research,* **21**: 1730−1741.

Lertzman KP. 1992. Patterns of gap-phase replacement in a subalpine old-growth forest. *Ecology,* **73**: 657−669.

Lertzman KP, Sutherland GD, Inselberg A, Saunders SC. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecology,* **77**: 1254−1270.

Levey DJ. 1988. Tropical wet forest treefall gaps and distribution of understory birds and plants. *Ecology,* **69**: 1076−1089.

Li QZ, Bogaert J, Nijs I. 2005. Gap pattern and colonization opportunities in plant communities: effects of species richness, mortality, and spatial aggregation. *Ecography,* **28**: 777−90.

Lima RAF, Martini AMZ, Gandolfi S, Rodrigues RR. 2008. Repeated disturbances and canopy disturbance regime in a tropical semi-deciduous forest. *Journal of Tropical Ecology,* **24**: 85−93.

Lin Y, Hulting ML, Augspurger CK. 2004. Causes of spatial patterns of dead trees in forest fragments in Illinois. *Plant Ecology,* **170**: 15−27.

Lindenmayer DB, Franklin JF. 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Washington: Island Press.

Liu QH, Hytteborn H. 1991. Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. *Journal of Vegetation Science,* **2**: 391−402.

Lundquist JE, Beatty JS. 2002. A method for characterizing and mimicking forest canopy gaps caused by different disturbances. *Forest Science,* **48**: 582-594.

Malcom DC, Mason WL, Clarke GC. 2001. The transformation of conifer forests in Britain- regeneration, gap size and silvicultural systems. *Forest Ecology and Management,* **151**: 7−23.

Marthews TR, Burslem DFRP, Phillips RY, Mullins CE. 2008. Modelling direct radiation and canopy gap regimes in tropical forests. *Biotropica,* **40**: 676−685.

McCarthy JW. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environmental Review,* **9**: 1−59.

McGuire JP, Mitchell RJ, Moser EB, Pecot SD, Gjerstad DH, Hedman CW. 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. *Canadian Journal of Forest Research,* **31**: 765−778.

Meyer P, Tabaku V, von Lüpke B. 2003. The structure of Albanian-beeches forests - derivations for a natural beech economy. *Forestry Science Central Journal,* **122**(1): 47−58.

Mercurio R. 1994. Esperienze sul trattamento delle abetine nelle foreste casentinesi. *Annali Istituto Sperimentale per la Selvicoltura XXII,* **1**: 95−116.

Mercurio R. 2000 Experiences and perspectives on the application of cutting a hole in the fir woods of the National Park of Casentino Forests.. *L'Italia Forestale e Montana,* **55**: 219−230.

Mercurio R. Spampinato G. 2001. Vegetation dynamics in a hole cut in the fir-woods of the National Park of Casentino Forests. *Informatore Botanico Italiano,* **33**: 215−218.

Messier C. 1996. Managing light and understory vegetation in boreal and temperate broadleaf-conifer forests. *In:* Comeau P.G. and K.D. Thomas (eds.), *Silviculture of Temperate and Boreal Broadleaf-Conifer Mixtures.* Victoria: B.C. Ministry of Forests, Research Program, pp. 59−81.

Midgley JJ, Cameron MC, Bond WJ. 1995. Gap characteristics and replacement patterns in the Knysna Forest, South Africa. *Journal of Vegetation Science,* **6**: 29−36.

Mihók B, Gálhidy L, Hagyó A, Standovár T, Rajkai K. 2004. Comparative studies of gap-phase regeneration in managed and natural beech forests in different parts of Europe: relations between tree regeneration and light, soil conditions, and ground vegetation. Part 5 - Case study partner report from Hungary. NatMan project WP3. Working Report 37. Deliverable 12 and 21.

Mihók B, Gálhidy L, Kelemen K, Standovár T. 2005. Study of gap-phase regeneration in a managed beech forest: relations between tree regeneration and light, substrate features and cover of ground vegetation. *Acta Silvatica & Lingaria Hungarica,* **1**: 25−38.

Muscolo A, Sidari M, Mercurio R. 2007a. Variations in soil chemical properties and microbial biomass in artificial gaps in Silver fir stands. *European Journal of Forest Research,* **126**: 59−65.

Muscolo A, Sidari M, Mercurio R. 2007b. Influence of gap size on organic matter decomposition, microbial biomass and nutrient cycle in Calabrian pine (*Pinus laricio* Poiret) stands. *Forest Ecology and Management,* **242**: 412−418.

Muscolo A, Mallamaci C, Sidari M, Mercurio R. 2011. Effects of gap size and soil chemical properties on the natural regeneration in black pine (*Pinus nigra,* Arn.) stands. *Tree Forest Science Biotechnology,* **5**: 65−71

Nagel TA, Svoboda M, Rugani T, Diaci J. 2010. Gap regeneration and replacement patterns in an old-growth *Fagus−Abies* forest of Bosnia- Herzegovina. *Plant Ecology,* **208**, 307−318.

Nakamura A, Morimoto Y, Mizutani YA. 2005. Adaptive management approach to increasing the diversity of a 30-year-old planted forest in an urban area of Japan. *Lands Urban Plan,* **70**: 291−300.

Nyland RD. 2002. *Silviculture: Concepts and Aplications, second ed.* Boston: McGraw Hill.

Nuske RS, Sprauer S, Saborowski J. 2009. Adapting the pair-correlation function for analysing the spatial distribution of canopy gaps. *Forest Ecology and Management,* **259**: 107−116.

Obiri JF, Lawes MJ. 2004. Chance versus determinism in canopy gap regeneration in coastal scarp forest in South Africa. *Journal of Vegetation Sci-*

ence, **15:** 539−547.

Ochiai Y, Okuda S, Sato A. 1994. The influence of canopy gap size on soil water condition in a deciduous broad-leaved secondary forest in Japan. *Journal of Japanese Forest Society*, **76:** 308−314.

Ogden J, Fordham RA, Pilkington S, Serra RG. 1991. Forest gap formation and closure along an altitudinal gradient in Tongariro National Park, New Zealand. *Journal of Vegetation Science*, **2:** 165−172.

Oldeman RAA. 1978. Architecture and energy exchange of dicotyledonous trees in the forest. *In*: Tomlinson P.B. and M.H. Zimmerman (eds), *Tropical Trees as Living Systems*. Cambridge: Cambridge University Press, pp. 535−560.

Ostertag R. 1998. Belowground effects of canopy gaps in a tropical wet forest. *Ecology,* **79:** 1294−1304.

Palik BJ, Mitchell RJ, Houseal G, Pederson N. 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. *Canadian Journal of Forest Research*, **27:** 1458−1464.

Parisi V. 2001. The biological quality of the soil. A method based on microarthropods. *Acta Naturalia de "L'Ateneo Parmense"*, **37:** 105−114.

Parsons WFJ, Knight DH, Miller SL. 1994. Root gap dynamics in lodgepole pine forest: nitrogen transformations in gaps of different size. *Ecological Applications*, **4:** 354−362.

Pedersen BS. Howard JL. 2004. The influence of canopy gaps on overstory tree and forest growth rates in a mature mixed-age, mixed-species forest. *Forest Ecology and Management*, **196:** 351−366.

Piussi P. 1994. Selvicoltura Generale. Utet, Torino.

Platt WJ, Strong DR. 1989. Special feature. Gaps in forest ecology. *Ecology*, **70:** 535−576.

Portoghesi L, Agrimi MG, Bollati S, Corona P, Ferrari B, La Monaca A, Plutino M. 2005. Observations on a high forest of oak and intervention hypotheses culture-oriented diversification of the structure and composition of the tree. *L'Italia Forestale e Montana*, **60:** 505−519.

Poulson TL, Platt WJ. 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology,* **77:** 1234−1253.

Prescott CE, Hope GD, Blevins LL. 2003. Effect of gap size on litter decomposition and soil nitrate concentrations in a high elevation spruce-fir forest. *Canadian Journal of Forest Research*, **33:** 2210−2220.

Qin X, Li G, Wang D, Liu R, Yang G, Feng Y, Ren G. 2011. Determinism versus chance in canopy gap herbaceous species assemblages in temperate *Abies–Betula* forests. *Forest Ecology and Management,* **262:** 1138−1145.

Raddi S, Basile L, Anichini M, Pozzim D, Logli F. 2009. Influenza della luce e dell'umidità del suolo sulla crescita e fisiologia della rinnovazione di farnia nelle radure di querceti misti. *Forest@,* **6:** 240-255. URL: http://www.sisef.it/forest@/.

Raymond P, Munson AD, Ruel JC, Coates KD. 2006. Spatial patterns of soil, microclimate, light, regeneration, and growth within silvicultural gaps of mixed tolerant hardwood–white pine stands. *Canadian Journal of Forest Research*, **36:** 639−651.

Rebertus AJ, Veblen TT. 1993. Structure and tree-fall gap dynamics of old-growth Nothofagus forests in Tierra del Fuego, Argentina. *Journal of Vegetation Science*, **4:** 641−654.

Ritter E. 2005. Litter decomposition and nitrogen mineralization in newly formed gaps in a Danish beech (*Fagus sylvatica*) forest. *Soil Biology and Biochemistry*, **37:** 1237−47.

Ritter E, Dalsgaard L, Einhorn KS. 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. *Forest Ecology and Management*, **206:** 15−33.

Ritter E, Vesterdal L. 2006. Gap formation in Danish beech (*Fagus sylvatica*) forests of low management intensity: soil moisture and nitrate in soil solution. *European Journal of Forest Research,* **125:** 139−150.

Robert A. 2003. Simulation of the effect of topography and tree falls on stand dynamics and stand structure of tropical forests. *Ecological Models*, **167:** 287−303.

Ross DJ, Speir TW, Tate KR, Cairns A, Meyrick KF, Pansier EA. 1982. Restoration of pasture after topsoil removal: effect of soil carbon and nitrogen mineralization, microbial biomass and enzyme activities. *Soil Biol0gy and Biochemistry*, **14:** 575−81.

Rouivinen S, Kouki J. 2011. Tree regeneration in artificial canopy gaps established for restoring natural structural variability in a Scots pine stand. *Silva Fennica*, **45:** 1079−1091.

Rugani T, Diaci J, Hladnik D. 2013. Gap dynamics and structure of two old-growth beech forest remnants in Slovenia. PLoS One 8(1): e52641. doi:10.1371/journal.pone.0052641.

Runkle JR. 1981. Gap regeneration in some old-growth forest of Eastern United States. *Ecology*, **62:** 1041−1051.

Runkle JR. 1985. Disturbance regimes in temperate forests. *In:* Pickett, S.T.A. and P.S. White (eds), *The Ecology of Natural Disturbance and Patch Dynamics*. New York: Academic Press, pp. 17−33.

Runkle JR. 1991. Gap dynamics of old-growth eastern forests: management implications. *Natural Areas Journal*, **11:** 19−25.

Runkle JR. 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. *Ecology,* **8:** 554−567.

Salvador-Van Eysenrode D, Bogaert J, Van Hecke P, Impens I. 1998. Influence of tree-fall orientation on canopy gap shape in an Ecuadorian rain forest. *Journal of Tropical Ecology*, **14:** 865−869.

Sapkota IP, Tigabu M, Oden PC. 2009. Species diversity and regeneration of old-growth seasonally dry *Shorea robusta* forests following gap formation. *Journal of Forestry Research*, **20:** 7−14.

Sariyildiz T. 2008. Effects of gap-size classes on long-term litter decomposition rates of beech, oak and chestnut species at high elevations in Northeast Turkey. *Ecosystems,* **11:** 841−853.

Scharenbroch BC, Bockheim JG, 2007a. Impacts of forest gaps on soil properties and processes in old growth northern hardwood-hemlock forests. *Plant and Soil,* **294:** 219−233.

Scharenbroch BC, Bockheim JG, 2007b. Pedodiversity in an old-growth northern hardwood forest in the Huron Mountains, Upper Peninsula, Michigan. *Canadian Journal of Forest Research,* **37:** 1106−1117.

Scharenbroch BC, Bockheim JG. 2008. Gaps and soil C dynamics in old growth northern hardwood-hemlock forests. *Ecosystems,* **11:** 426−441.

Schliemann S, Bockheim JG. 2011. Methods for studying treefall gaps: A review. *Forest Ecology and Management*, **261:** 1143−1151.

Schnitzer SA, Mascaro J, Carson WP. 2008. Treefall gaps and the maintenance of plant species diversity in tropical forests. *In:* Carson W.P. and S.A. Schnitzer (eds.), *Tropical Forest Community Ecology*. Chichester: Blackwell, pp. 196−209.

Schumann ME, White AS, Witham JW. 2003. The effects of harvest-created gaps on plant species diversity composition, and abundance in a Maine oak-pine forest. *Forest Ecology and Management*, **176:** 543−561.

Seymour RS, White AS, de Maynadier PG. 2002. Natural disturbance regimes in northeastern North America-evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management*, **155:** 357−367.

Silver WL, Vogt KA. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *Journal of Ecology*, **81:** 729−738.

Singh JS, Raghubanshi AS, Singh RS, Srivastava C. 1989. Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. *Nature*, **338:** 499−500.

Sipe TW, Bazzaz FA. 1995. Gap partitioning among maples (*Acer*) in central New England: survival and growth. *Ecology*, **76:** 1587−1602.

Smith JL, Paul EA. 1990. The significance of soil microbial biomass estimations. *In:* Bollag J.M. and G. Stotzky (eds), *Soil Biochemistry*. New

York: Marcel Dekker Inc, pp. 357−396.

Smith JL, Papendick RI, Bezdicek DF, Lynch JM. 1993. Soil organic matter dynamics and crop residue management. *In:* Metting F.B. Jr (ed), Soil Microbial Ecology. New York: Marcel Dekker Inc., pp.65v94.

Spiecker H, Hansen J, Klimo E, Skovsgaard JP, Sterba H, von Teuffel K. 2004. Norway spruce conversion. Options and consequences. EFI Research Report n. 18. S. Brill Academic Publishers, Leiden.

Spies TA, Franklin JF, Klopsch M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research*, **20:** 649−658.

Taylor BR, Parsons WJF, Parkinson D. 1989. Decomposition of *Populus tremuloides* leaf litter accelerated by addition of *Alnus crispa* litter. *Canadian Journal of Forest Research*, **19:** 674−679

Tews J, Brose U, Grimm V, Tielborger K, Wichmann M, Schwager M, Jeltsch F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31:** 79−92

van Couwenberghe R, Collet C, Lacombe E, Pierrat JC, Gégout JC. 2010. Gap partitioning among temperate tree species across a regional soil gradient in windstorm-disturbed forests. *Forest Ecology and Management*, **260:** 146−154.

van Dam O. 2001. Forest filled with gaps: effects of gap size on water and nutrient cycling in tropical rain forest – a study in Guyana. Tropenbos Guyana Program, Georgetown, 208 pp.

Van der Maarel E. 1988. Vegetation dynamics: patterns in time and space. *Vegetatio,* **77:** 7−19

Van der Meer PJ, Bongers F. 1996. Formation and closure of canopy gaps in the rain forest at Nouragues, French Guiana. *Vegetatio*, **126:** 167−79.

Van der Meer PJ, Dignan P, Savenh AG. 1999. Effect of gap size on seedling establishment, growth and survival at three years in mountain ash (*Eucalyptus regnans* F. Muell.) forest in Victoria, Australia. *Forest Ecology and Management*, **117:** 33−42.

Veenendal EM, Swaine MD, Agyeman VK, Blay D, Abebrese ID, Mullins CE. 1996. Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology*, **83:** 83−90.

Vetaas OR. 1997. The effect of canopy disturbance on species richness in a central Himalayan oak forest. *Plant Ecology*, **132:** 29−38.

Vitousek P, Denslow JS. 1986. Nitrogen and phosphorus availability in tree fall gaps in a lowland tropical rainforest. *Journal of Ecology*, **74:** 1167−1178.

Xi W, Pee, RK, Urban DL. 2008. Changes in forest structure, species diversity and spatial pattern following hurricane disturbance in a Piedmont North Carolina forest, USA. *Journal of Plant Ecology,* **1:** 43−57.

Wang G, Liu F. 2011.The influence of gap creation on the regeneration of *Pinus tabuliformis* planted forest and its role in the near-natural cultivation strategy for planted forest management. *Forest Ecology and Management*, **262:** 413−423.

Waring RH, Schlesinger WH. 1985. Forest ecosystems: concepts and management. Academic Press, Orlando, USA. pp.440.

Watt AS. 1947. Pattern and process in the plant community. *Journal of Ecology,* **35:** 1−22.

White PS, Pickett STA. 1985. Natural disturbance and patch dynamics: an introduction, *In*: Pickett S.T.A and P.S. White (eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. San Diego: Academic Press, pp. 3−13.

Whitmore TC. 1982. On pattern and process in forests. *In*: Newman E.I. (ed), *The Plant Community as a Working Mechanism*. Oxford: Blackwell Scientific Publications, pp.45−59.

Whitmore TC. 1989. Canopy gaps and the two major groups of forest trees.

Ecology, **70:** 536−538.

Woods KD. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *Journal of Ecology*, **92:** 464−476.

Wright EF, Coates KD, Bartemucci P. 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. Canadian *Journal of Forest Research*, **28:** 1352−1364.

Wright SJ. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130:** 1−14.

Yamamoto SI. 1992. The gap theory in forest dynamics. *Botanical Magazine, Tokio* **105:** 375−383.

Yamamoto S. 1994. Gap regeneration in primary evergreen broadleaved forests with or without a major canopy tree, *Distylium racemosum*, southwestern Japan: A comparative analysis. *Ecological Research*, **9:** 295−302.

Yamamoto S. 1995. Gap characteristics and gap regeneration in subalpine old-growth coniferous forest, central Japan. *Ecological Research*, **10:** 31−39.

Yamamoto S. 1996. Gap regeneration of major tree species in different forest types of Japan. *Vegetatio*, **127:** 203−213.

Yamamoto SI. 2000. Forest gap dynamics and tree regeneration**.** *Journal of Forest Research,* **5:** 223−229.

Yamamoto S, Nishimura N, Torimaru T, Manabe T, Itaya A, Becek K. 2011. A comparison of different survey methods for assessing gap parameters in old-growth forests. *Forest Ecology and Management*, **262:** 886−893.

Zang RG, Tao JP, Li CY. 2005. Within community patch dynamics in a tropical montane rain forest of Hainan Island, South China. *Acta Oecologica*, **28:** 39−48.

Zang RG, Wang BS. 2002. Study on canopy disturbance regime and mechanism of tree species diversity maintenance in the lower subtropical evergreen broad-leaved forest, South China. *Plant Biosystems,* **136:** 241−50.

Zeng DH, Hu YL, Chang SX, ZP. 2009. Land cover change effects on soil chemical and biological properties after planting Mongolian pine (*Pinus sylvestris* var. mongolica) in sandy lands in Keerqin, northeastern China. *Plant and Soil,* **317:** 121v33.

Zhang Q, Liang Y. 1995. Effects of gap size on nutrient release from plant litter decomposition in a natural forest ecosystem. *Canadian Journal of Forest Research*, **25:** 1627−1638.

Zhang XR, Tan XF, Wang RQ, Xu NN, Guo WH. 2013. Effects of soil moisture and light intensity on ecophysiological characteristics of *Amorpha fruticosa* seedlings. *Journal of Forestry Research* **24:** 293−300.

Zhang QH, Zak J. 1995. Effects of gap size on litter decomposition and microbial activity in a subtropical forest**.** *Ecology*, **76:** 2196−2204.

Zhu JJ, Matsuzaki T, Lee FQ, Gonda Y. 2003. Effect of gap size created by thinning on seedling emergency, survival and establishment in a coastal pine forest. *Forest Ecology and Management,* **182,** 339−354.

Zhu JJ, Tan H, Li FQ, Chen M, Zhang JX. 2007. Microclimate regimes following gap formation in a montane secondary forest of eastern Liaoning Province, China. *Journal of Forestry Research*, **18**(3): 167−173.

Zhu JJ, Lu DL, Zhang WD. 2014. Effects of gaps on regeneration of woody plants: a meta-analysis. *Journal of Forestry Research*, **25**(3): 501−510.

Zirlewangen D, von Wilpert K, 2001. Modelling water and ion fluxes in a highly structured, mixed-species stand. *Forest Ecology and Management*, **143:** 27−37.